netic as the porphyrin itself; they conclude, as do we, that the nickel porphyrins contain no unpaired electrons.

[1] For a summary of the history of the hemochromogen problem see M. L. Anson and A. E. Mirsky, *Physiol. Rev.*, **10**, 506 (1930).

[2] M. L. Anson and A. E. Mirsky, *Jour. Physiol.*, **60**, 50 (1925); *Jour. Gen. Physiol.*, **12**, 273 (1928).

[3] L. Pauling, *Jour. Am. Chem. Soc.*, **53**, 1367 (1931); **54**, 988 (1932).

[4] This interpretation of the magnetic data is supported by chemical analyses, which correspond to two pyridine groups for each heme in pyridine hemochromogen (R. Hill, *Proc. Roy. Soc.*, **B100**, 419 (1925)) and to two cyanide ions for each heme in dicyanide hemochromogen (M. L. Anson and A. E. Mirsky, *Jour. Gen. Physiol.*, **14**, 43 (1930)).

[5] H. Fischer and B. Pützer, *Zeit. physiol. Chem.*, **154**, 39 (1926).

[6] R. B. Janes, *Jour. Am. Chem. Soc.*, **57**, 471 (1935).

[7] R. G. Dickinson, *Ibid.*, **44**, 2404 (1922); B. N. Dickinson, *Zeit. Krist.*, **88**, 281 (1934).

[8] E. G. Cox and K. C. Webster, *Jour. Chem. Soc.*, **1935**, 713; J. M. Robertson, *Ibid.*, **1935**, 615; D. Harker, *Z. Krist.*, **93**, 136 (1936).

[9] D. Keilin, *Proc. Roy. Soc.*, **B100**, 129 (1926).

[10] J. H. Van Vleck, *Electric and Magnetic Susceptibilities*, Oxford University Press, 1932, p. 228.

[11] R. Willstätter and Y. Asahina, *Ann.*, **385**, 197 (1911).

[12] F. Haurowitz and H. Kittel, *Ber.*, **66**, 1046 (1933).

[13] L. Cambi and L. Szegö, *Rend. ist. lombardo sci.*, **67**, 275 (1934).

[14] R. Hill, *Biochem. Jour.*, **19**, 341 (1925).

[15] M. L. Anson and A. E. Mirsky, *Jour. Gen. Physiol.*, **14**, 43 (1930).

[16] F. Haurowitz and W. Klemm, *Ber.*, **68**, 2312 (1935).

SEGREGATION OF COLOR AND GROWTH-REGULATING GENES IN SOMATIC TISSUE OF MAIZE

BY DONALD F. JONES[1]

CALIFORNIA INSTITUTE OF TECHNOLOGY, PASADENA, CALIFORNIA

Communicated January 16, 1936

A microscopical examination of mature seeds of *Zea mays* in a number of different lines has shown a surprisingly large number of color and growth mosaics in aleurone and endosperm tissue. Maize endosperm is unusually favorable material in which to study genetic changes in somatic tissue. It is a short-lived, food-storage structure. Changes can occur late in development with no serious injury to the young seedling. Consequently aberrations have not been selected against as severely as in other parts of the organism.

Mosaics do occur in plant tissues involving known genes but are rare. A sterile abnormal sector has been found in the pistillate inflorescence of maize that developed at a faster rate than the normal tissue on either side. This overgrowth has the appearance of a genetic mosaic. The normal

seeds from the same plant have not reproduced this type of aberration but have given indications of sporadically recurring tissue irregularities in a few of the descendants.

Alterations in endosperm tissue are much more frequent than in the plant tissue and are expressed in many different ways when dominant genes are received from only the pollen parent. From a large amount of material showing mosaics a few ears are selected which demonstrate the various types of genetic changes that may occur. The results are given in table 1. All of the seeds in these six progenies are *c c C* in aleurone composition and are normally purple in color. Uncolored areas are found on about one fifth of these seeds ranging in size from large white patches occupying from one third to one half the surface of the seed down to single colorless cells. Mosaics having a few cells altered in color are much more frequent than large areas. Many small mosaics may be found on a single seed. The few cell and single cell mosaics are not so easily seen in this material as in the reverse color change involving the dominant aleurone color inhibitor, C^I, when it is paired with C^iC^i. In such seeds colored cells appear among normally colorless cells and are quite conspicuous with low magnification. These mosaics are surprisingly frequent in some families. In a few progenies, mosaics comprising one or more cells have been found on every seed and some seeds have ten or more different mosaics. This gene combination does not show the other types of changes that occur in heterozygous *c c C* seeds listed in table 1.

TABLE 1

TYPES OF MOSAICS IN MAIZE ENDOSPERM

PEDIGREE NO.	TOTAL NO. OF SEEDS	NUMBER OF SEEDS SHOWING MOSAICS AREAS AS FOLLOWS, UNCOLORED AREAS	UNCOLORED PAIRED WITH DARK COLORED AREAS	LARGE DARK CELLS	DEPRESSED AREAS	OUTGROWTHS
849 × 626	376	69	8	3	2	2
563 × 626	158	52	2	3	1	2
463 × 626	417	77	13	31	13	3
463 × 626	285	51	8	4	4	1
904 × 76	196	81	17	15	2	1
904 × 489	374	144	26	..	5	3
Totals	1806	474	74	56	27	12

Along with the colorless mosaic areas in tissue that is normally colored there are also paired mosaics usually referred to as twin spots. In Drosophila twin spots show when dominant linked genes are involved and are assumed to result from somatic crossing-over. In maize endosperm, linked genes cannot be used to show paired mosaics because this tissue is $3N$ in composition and it is therefore impossible to have single dominant genes from both parents. Paired mosaics in maize appear when different numbers of the same alleles have a visible effect. Such a condition has

been found to result from the *C* aleurone color gene and the *P* pericarp color gene.

Paired stripes of pericarp tissue that are darker and lighter in color than normal have been found in a self-colored variety of maize (Sweepstakes) having a light colored pericarp. These are similar to the twin stripes in fruit and flower epidermis in many species.

Many clear twin spots have been found in aleurone color involving the *C* gene. These are listed in the fourth column of table 1. They occur as uncolored areas adjoining colored areas that are distinctly darker than the normally colored aleurone surrounding them. The borders of these darker areas are clearly defined. These paired mosaic areas have developed from single cells at the start in which genic segregation has taken place. The change from light to dark color coincides with the removal of the dominant *C* gene from the single cell that is the progenitor of the colorless area. Reciprocal combinations of the *c* and *C* genes normally differ in color because two doses of *C* from the seed parent make the seeds darker than the one dose from the pollen parent. The darker area in the twin spots therefore can be due to the addition of the one *C* gene that is removed from the uncolored area.

In the majority of cases the paired colorless and darker areas are normal in growth and are approximately equal in area. In some progenies there is a noticeable tendency for the one area to be smaller in size than the other. In a few cases some of the darker areas later lose all color in some cells and a mixture of colorless and darker colored cells is seen in the colored part of the twin spot. In a number of cases the darker cells are distinctly larger than the normal cells around them.

In progenies where twin spots occur, clearly defined areas of larger and darker cells than normal are easily seen. The change may take place both in size and color of cells or in either alone. In most cases the larger cells are also darker. In these areas there is no accompanying change to light colored or colorless cells as in the twin spots.

Nearly all progenies that show these different types of color mosaics also show a smaller proportion of growth changes manifested in depressed areas and in outgrowths. The depressed areas are small, pit-like cavities, resembling small sugary mosaics. The sugary gene is not involved in this material and mosaics of this type are not expected. Considerable tissue develops which later breaks down or shrinks at maturity.

The outgrowths vary in area and extent to which the cells are raised above the surrounding tissue. They may be less than one to several millimeters in diameter and are raised about one fourth as high as wide. Some of them are distinct tumor-like projections. They are apparently not due to injury or infection since the pericarp overlaying them is usually intact and not discolored. In the larger outgrowths the pericarp is split and some-

times discolored. These outgrowths occur in self-fertilized seeds and in out-crosses. They have been found on a few seeds in the second generation of a family that showed similar mosaics. In several cases, outgrowths and depressions occur as paired mosaics, the raised area adjoins, on one side, an area that is depressed below the surrounding normal tissue. Both depressed and raised areas have been found adjoining or coinciding with color changes.

That there are growth-regulating genes in the chromosomes is evident from the fact that differences in sizes and shapes in plants and animals are transmitted from one generation to another and these different forms are capable of recombination with other characters and in some cases show linkage with known qualitative genes. The evidence indicates that in these growth mosaics, cell-coördinating genes are either lost or are shifted from cell to cell in growing somatic tissue in the same way that color genes are.

Since simple color changes have been found on the same seeds with paired color mosaics and with larger-cell areas and darker-cell areas alone, obviously different genetic changes are involved in these varying phenomena. In the first case a dominant gene is removed from one cell and is not added to an adjoining cell that survives and reproduces itself. This loss from one chromosome does not prevent normal cell division and growth. It has been shown that linked genes may or may not be lost simultaneously from a mosaic area. The loss of a series of linked genes could be due either to non-disjunction, somatic crossing-over of homologous chromosomes, reciprocal translocation (non-homologous crossing-over), translocation or deletion. The los sof some linked genes and not others cannot be due to non-disjunction. Mosaics involving genes near the ends of the chromosomes occur more frequently than those near the spindle attachment.

The paired mosaics (twin spots and twin stripes) result from either non-disjunction, somatic crossing-over (homologous or non-homologous) or translocation. In seeds that are heterozygous for both *C* and *Pr*, well-defined red and white twin spots occur. These result from an interchange between chromosomes 5 and 9 removing *C* from one daughter cell and *Pr* from the other. Other types of paired mosaics also appear. Non-homologous crossing-over in this way, in time, can remove any gene from certain cells in somatic tissue. No direct evidence is at hand to show what genetic changes accompanying the tissue alterations except that they do occur at the same stages of development, in approximately the same order of frequency and are similar in size and outline to the changes involving known genes. The exact mode of their occurrence is not so important for the present as the fact that growth changes do occur as a result of somatic segregation.

[1] Research Fellow in the William G. Kerckhoff Laboratories while on leave from the Connecticut Agricultural Experiment Station, New Haven, Connecticut.